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The effect of root uptake by Myriophyllum spicatum on temporal and
spatial distributions of bioavailable phosphorus in a littoral sediment

University — Université

Carleton

Degree for which thesis was presented — Grade pour lequel cette thèse fut présentée

M.Sc.

Year this degree conferred — Année d'obtention de ce grade

1983

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THE EFFECT OF ROOT UPTAKE BY MYRIOPHYLLUM SPICATUM ON
TEMPORAL AND SPATIAL DISTRIBUTIONS OF BIOAVAILABLE
PHOSPHORUS IN A LITTORAL SEDIMENT

by

© ELEANOR JEAN ZURBRIGG BOTTOMLEY, B.Sc.

A thesis submitted to the Faculty of
Graduate Studies and Research in partial fulfilment
of the requirements for the degree of
Master of Science

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ABSTRACT

Plant uptake of sediment bioavailable phosphorus was assessed in relation to the temporal and spatial distributions of the dissolved and adsorbed phosphorus phases in a littoral sediment in Lake Opinicon, Ontario. From June to October 1981, profiles of soluble reactive phosphorus (SRP) were measured in the interstitial water of a milfoil- (Myriophyllum spicatum) colonized sediment and in a sediment denuded of plants, using an in situ dialysis technique. SRP concentrations in the denuded sediment increased during the summer and peaked in late summer. Profiles of SRP collected in the weedbed sediment generally did not vary through time, indicating that milfoil roots took up SRP from the interstitial water as it became available during the summer. Adsorbed bioavailable phosphorus, analysed in sediment cores, followed the same trend as the dissolved phase (SRP). Within the root zones of individual milfoil plants, depletion contours of SRP extended to 36 cm to 50 cm depth in the sediment, and laterally to 12 cm to 20 cm about the root crown. These findings are discussed in relation to internal cycling of phosphorus in the littoral zone.

ACKNOWLEDGEMENTS

This study was carried out under the supervision of Dr. I.L. Bayly of Carleton University, whose support and encouragement throughout the study was greatly appreciated. Financial support was given to Dr. Bayly from a research grant from Graduate Studies and Research, Carleton University, and through contract projects with Canada Centre for Inland Waters, Burlington, Ontario. I also thank Dr. H.G. Merriam for input of ideas, advice and constructive criticism at various stages of this study. Drs. C.A. Barlow and J.D.H. Lambert were also helpful. I thank Dr. Roland Thomas for statistical advice.

G.C. Bayly drafted most of the figures, for which I am most grateful. S. Wendt critically read the final draft of this thesis, which was much appreciated.

Without the help of Dave Omond this study could not have been carried out. Dave's long hours spent SCUBA diving in the murky weedbed were greatly appreciated. J. Middleton generously volunteered his services in the field, and for this I am grateful. M. Henderson and others assisted on occasion.

F. Phelan and other staff at the Queen's University Biology Station provided the facilities, boats, etc. on which the field work depended, and this was appreciated.

A special thanks is also due to the Science Workshops at Carleton University for their skilful construction of both models of the dialysis sampler. D. Omond assisted with technical details of the design of the cylindrical dialysis sampler, and with drafting modifications to the rectangular sampler.

I thank J. Gale for performing the phosphorus analyses on plant and sediment core samples.

Finally, I would like to thank D. Bottomley for his perseverance, support, encouragement (and many geochemical references) throughout all phases of the study.

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1. INTRODUCTION

One of the basic problems in evaluating the role of submerged macrophytes in phosphorus cycling is the determination of the relative importance of roots versus shoots in phosphorus uptake. The predominance of shoots in nutrient uptake of submerged macrophytes is suggested by the physiological adaptations of submerged leaves for nutrient uptake and by the low root/shoot ratio. Recent studies have indicated that root uptake may predominate in phosphorus uptake in many cases (Bristow and Whitcombe 1971, Denny 1980, Carignan 1982 and references therein). Almost exclusive root uptake of phosphorus from sediments has been demonstrated for Eurasian Watermilfoil (Myriophyllum spicatum L.) grown under laboratory conditions (Bole and Allan 1978) and in situ (Carignan and Kalff 1980) where concentrations of dissolved inorganic phosphate in the overlying water were low.

Sediment phosphorus absorbed by milfoil roots is transferred to the growing shoot (Barko and Smart 1980, Carignan and Kalff 1980), and eventually released to the overlying water upon decomposition of the plant (Landers 1982). In lakes having dense growths of submerged macrophytes such as milfoil, the weedbeds may be an important pathway for internal cycling of available phosphorus, thus stimulating productivity of the open waters.

The spread of M. spicatum into Canadian lakes

(Aiken et al. 1979) and concern over management of this plant necessitates a better understanding of its nutrient relationships. Harvesting programs aimed at nutrient removal require quantification of the phosphorus pool available for uptake.

While radiotracer uptake studies (see Carignan 1982 and references therein) show that M. spicatum takes up sediment phosphorus, little is known of the actual depths in lake sediments from which this phosphorus is derived, or of the relative availability to macrophytes of different phosphorus forms in sediments, or of the seasonal availability of sediment phosphorus forms.

Interstitial (pore) waters in sediments are often enriched with phosphorus relative to the overlying water. Phosphorus dissolved in the interstitial water is in a dynamic equilibrium with phosphorus adsorbed on the particulate phase (Li et al. 1972). Characteristic vertical concentration gradients of dissolved phosphate develop in the interstitial water of anoxic sediments as a result of chemical and physical processes (Lerman 1977, 1979) involving production, removal and transport of phosphate. In organic-rich sediments, the concentration of dissolved phosphate in the interstitial waters is mainly controlled by decomposition of organic matter (phosphate production) and reversible linear adsorption processes (uptake and release) (Berner 1977). Interstitial water profiles of dissolved phosphate should thus

3
be a sensitive indicator of decomposition.

I measured pore water profiles of dissolved phosphate and sediment column profiles of adsorbed phosphate in a milfoil-colonized sediment and a denuded sediment from spring until fall, and lateral-vertical profiles of pore water phosphate concentrations within the root zone of individual milfoil plants. Utilization of bioavailable phosphorus forms by milfoil can be demonstrated as the difference between the two sediment conditions (plants, no plants), and by the existence of depletion contours of phosphate within the root zone of individual plants. The temporal and vertical distributions of dissolved and adsorbed bioavailable phosphorus can also be assessed from this information.

2. MATERIALS & METHODS

2.1 Experimental Design

Levels of dissolved inorganic phosphate in the sediment interstitial water were monitored within a milfoil weedbed and an area denuded of plants. The denuded sediment was a 50 m by 50 m area within the weedbed which was experimentally cleared of all macrophytes by uprooting and removal. Part of the denuded sediment had been cleared previously (summer 1980) as part of another study (Schut 1981). Both weedbed and denuded sediments were sampled at two to three week intervals from June to October 1981, for a total of 8 sampling events. The denuded sediment was re-sampled in June 1982 as a check on spring conditions.

The weedbed was divided into 8 sites, and 1 site was sampled per sampling event, (Fig. 1). This approach assumed overall homogeneity of sediments throughout the weedbed. The approach permitted harvesting of plants following sampling of interstitial waters, and conserved travel time. The site was marked by a float and 7 plants were selected in the area. Duplicate interstitial water samples were collected from the root zone of each plant for a total of 14 samples for each of the first 6 sampling events. Single samples per plant were collected for the final 2 samplings. Samplers were placed on opposite

FIGURE 1

Sampling sites within the milfoil weedbed

Numbers represent the date the location was sampled:

1 - June 16	5 - August 12
2 - June 30	6 - September 3
3 - July 14	7 - September 22
4 - July 28	8 - October 9
- D = denuded sediment area

sides of the milfoil root crown at a distance of about 5 cm from the plant. In the denuded sediment, 7 interstitial water samples were collected at intervals throughout the area.

Sediment cores for analysis of bioavailable phosphorus were collected in June, July and August 1981. Core were collected near sites sampled for interstitial waters, but one week later than the corresponding interstitial water samples.

A sampling technique for determining the spatial influence of an individual milfoil root mass on concentrations of interstitial phosphate was tested in September and October 1981, and again in May 1982.

The pool of phosphorus contained in milfoil shoot tissue was monitored from May to October 1981. Ten whole plants were collected each week, including the 7 plants used for interstitial water sampling when appropriate.

2.2 Experimental Procedure

2.2.1 The Study Area

Lake Opinicon (Leeds Co. and Frontenac Co., Ontario) is a shallow (mean depth = 4.9 m), hardwater (alkalinity = $90 \text{ mg CaCO}_3 \cdot \text{L}^{-1}$), mesotrophic lake on the Rideau Waterway. In 1832 the lake was enlarged by flooding, increasing the depth by about 3 m (Crowder et al. 1977).

Seventy percent of the lake is less than 3 m deep (Turnbull 1975). The north shore is mostly crystalline limestone, while the south shore is gneiss, granite and diorite, and there are some sandstone outcrops (Wynne Edwards 1959). There is a shallow, non-calcareous, well-drained sand in the vicinity of Cow Island (Ontario Ministry of the Environment 1971). The available physicochemical information on Lake Opinicon is summarized by Crowder et al. (1977).

Sampling was carried out in a sheltered, quiet, shallow bay (mean depth = 1.6 m) north of Cow Island and south of the inflow at Chaffey's Locks (Fig. 2). The shoreline of the bay is gently sloping, and is vegetated with deciduous trees and meadow. The bay is flooded land that is studded underwater with tree stumps, and is heavily vegetated with submerged and floating-leaved aquatic species. Myriophyllum spicatum is the dominant species (50 to over 75% surface cover), but may occur in association with Vallisneria americana, Potamogeton robbinsii, P. amplifolius, P. pectinatus and Ceratophyllum. M. spicatum invaded the lake in the early 1970's, and gradually increased in frequency to form largely monodominant stands in many areas of the lake (Crowder et al. 1977), particularly in the offshore 2.0 to 3.5 m zone (Keast 1983). Milfoil stands in Lake Opinicon were mapped in 1980 (Alvo 1981). Milfoil density is thought to be decreasing now in many stands.

FIGURE 2

Study site in Lake Opinicon, Ontario

OPINICON LAKE

Lake Opinicon sediments were studied by Curran (1947) for chemical composition, and by Brown (1952) for total phosphorus, soluble phosphorus, ammonia-nitrogen and organic carbon content. Keast (1983) described the substrate beneath M. spicatum communities as consisting of organic ooze, 0.2 to 0.4 m deep over a firm bottom, having a high clay content with particle size diameter ≤ 0.005 mm.

In the weedbed sediments that I studied, unconsolidated materials were 0.6 m deep over a firm bottom. Water content (porosity) was very high, being over 95% by weight near the sediment-water interface, decreasing to 90% at 30 cm and 70% at 40 cm depth in the sediment. The organic matter content of the sediment, determined as loss on ignition at 500°C for 5 h, was 66% throughout the top 20 cm layer, increasing to 82% at 24 cm depth, and decreasing to 54% at 36 cm depth. Sediment colour, based on the Munsell Soil Color Charts (1954), was a very dark grayish brown (2.5Y 3/2, dry) in the top 23 cm, grading to a very dark grayish brown (10YR 3/2) between 24 and 31 cm, to black (10YR 2/1) between 32 and 38 cm, and becoming gray (10YR 5/1) between 38 and 40 cm. A layer of wood chips at about 28 to 30 cm depth in the sediment probably dates this layer to 1832 when the area was flooded. The high organic content of these sediments should reflect the influence of organic sedimentation from the aquatic macrophytes, planktonic production and

the deciduous trees along the shore.

The effect on the system of the inflow at the locks is probably limited, as the current is restricted to the main channel in summer (Crowder et al. 1977).

2.2.2 Inorganic Phosphate Gradients in Interstitial Water

2.2.2.1 Vertical Gradients

Interstitial waters were sampled for dissolved inorganic phosphate using a compartmented dialysis sampler (Hesslein 1976) (Fig. 3). This in situ sampler is suitable for obtaining estimates of small-scale vertical distributions of chemical constituents in interstitial water. The sampler delivers twenty 10 ml sub-samples representing successive 2 cm vertical sampling intervals in the sediment. The sampler is made of plexiglas and measures 44 cm by 8 cm by 1 cm. Sampling interstitial water by dialysis eliminates problems associated with extraction of pore water from anoxic sediments (for example, Bischoff et al. 1970, Bray et al. 1973, Loder et al. 1978, Lyons et al. 1979).

The dialysis sampler operates on the principle that distilled water in the sampler compartments is separated by a semi-permeable membrane (dialysis membrane) from the sediment interstitial water and is allowed to come to equilibrium with the latter as ions

FIGURE 3

A modified version of an in situ compartmented dialysis sampler described by Hesslein (1976).

Rubber septa were added along the sides of the sampler for filling and emptying sampler compartments without damaging the membrane.

Scale: $\frac{3}{4}$ in = 4 cm

Also shown is one 'stacker' from another dialysis sampler.

0
2
4
cm

diffuse across the membrane into the distilled water, based on Fick's second law of diffusion modified for sediments (Berner 1971). Diffusivities in sediment pore waters vary with temperature, ion type, porosity, tortuosity and ion exchange reactions (Manheim 1970).

Samplers were fitted with a sheet of biologically inert polysulfon dialysis membrane (Gelman HT 450, pore size $0.45 \mu\text{m}$), filled with glass distilled, deionized water, deoxygenated by overnight equilibration in a closed bath of distilled water through which nitrogen gas had been bubbled, and sealed in the water bath for transport to the study site. Samplers were placed in the sediment by hand by a SCUBA diver and left 14 days to equilibrate, which was adequate for complete equilibration of samples with respect to phosphate concentration (see Appendix I). Omission of the deoxygenation pretreatment of samplers prior to insertion in the anoxic sediment did not affect measured dissolved phosphate concentrations (see Appendix I). The deoxygenation step was maintained to be consistent with early sampling procedures.

Upon removal from the sediment, dialysis samplers were rinsed with lake water, set on their sides, and the interstitial water samples removed through the rubber septa using 10 cc syringes fitted with 20G needles. The sample was transferred immediately to a pre-acidified polyethylene tube ($50 \mu\text{l}$ 1 N H_2SO_4) and stored near 4°C . On average, 6 minutes elapsed from removal of the sampler

from the sediment until all 20 chambers were emptied and acidified. Acidification of anoxic samples prevents oxidation and precipitation of iron and associated dissolved phosphate (German Chemists Association 1981). Acidification did not cause hydrolysis of dissolved organic phosphate during short-term storage (see Appendix II).

Dissolved inorganic phosphate (orthophosphate) was assayed manually by the ascorbic acid - molybdate method of Stainton et al. (1977) using a Bausch & Lomb Spectronic 70 with a 1 cm path length. The assay represents soluble reactive phosphate (hereafter SRP).

The 2 cm vertical sampling interval was sufficiently close with respect to changes in concentration of SRP with depth, to permit omission of every second dialysis chamber from SRP analysis except near the sediment-water interface. All samples were analysed near the interface. Thus SRP was determined for the interval covering 2 cm above the sediment-water interface, and below the interface, intervals 0-2 cm, 2-4 cm, 4-6 cm, 8-10 cm, 12-14 cm, etc. SRP concentrations for the omitted chambers were interpolated from the adjacent samples above and below.

SRP concentrations for corresponding depth intervals were averaged for the 2 samplers collected from each milfoil root zone, yielding 7 average profiles per sampling event. Data for SRP profiles were collapsed

into 5 depth classes: 0-8 cm, 8-16 cm, 16-24 cm, 24-32 cm, and 32-34 cm (weedbed) or 32-38 cm (denuded). The lower depth class was truncated since samplers were not all inserted to equal depths in the sediment. For each of these 5 depth classes, a one-way analysis of variance was performed to test for overall difference of mean SRP concentration with time. Where an overall difference was established, then the source of the difference was sought by testing each single comparison by pairwise t tests. Welch's separate variance t test was used, and the results evaluated by Bonferroni probabilities (Dixon et al. 1981). The Bonferroni test conservatively adjusts for the simultaneous comparison of all possible means by dividing the level of significance by the number of comparisons. For my data, the 8 means are compared as 28 different pairs. Therefore, for a given pairwise comparison to be significant at the overall .05 level, the P value of the t test must be less than $.05/28$ or .001786. Given the conservative nature of the Bonferroni test, a less restrictive overall error rate was selected (10%). The P value of the t test was therefore $.10/28$ or .00357. I felt that this error rate was appropriate for my study, in which the purpose was to look for pattern in the data, and in which the variability in the data was considered to represent real variability in the system being studied.

2.2.2.2 Lateral-Vertical Gradients Within Milfoil Root Zones

In order to sample SRP gradients simultaneously in 2 dimensions in a milfoil root zone, it was necessary to substantially modify the dialysis sampler. A narrow (3 cm) cylindrical design was adopted. By using several companion samplers deployed along a short transect passing outwards from a milfoil root crown (Fig. 4), both horizontal and vertical gradients of dissolved nutrients within the root zone were obtained.

The cylindrical dialysis sampler (Fig. 5) was externally similar to a dialysis sampler described by Mayer (1976) who used a perforated Lexan sleeve to house the dialysis materials. My sampler was compartmented internally by stacking small vials in the Lexan sleeve, an idea reminiscent of the 'rack of vials' mentioned by Schindler et al. (1977). Each vial has 3 side ports which are covered by a sheet of inert dialysis membrane, and septa in the ends for filling and emptying the vial by hypodermic syringe. Each vial delivers a 10 to 12 ml water sample which represents an in situ horizontal interval of 2 cm, and alternate 2 cm vertical intervals such that data are integrated over 4 cm vertical (depth) intervals. As constructed, the cylindrical sampler is 44 cm in length, but can be extended by threading together several sections of sleeve. Construction details are given in

FIGURE 4

Technique for simultaneously sampling lateral
and vertical concentration gradients in the inter-
stitial water in a milfoil root mass

AIR-WATER INTERFACE

FIG. 5

Cylindrical dialysis sampler

Components of the sampler include the perforated Lexan sleeve, ten unit containers or 'stackers,' (shown with and without dialysis membrane in place), O-rings and rubber septa. Samplers were marked by tying a painted cork to a length of fishing line attached to the top of the sampler, adjusted to keep the cork submerged.

Scale: 1 in = 6 cm

0
4
8
cm

Appendix III.

2.2.3 Bioavailable Phosphorus Gradients in Sediment Cores

Short cores of about 30 cm length were collected by hand using 6.5 cm diameter plexiglas tubing. Cores were sectioned into 2 cm intervals using a vertical extrusion technique. The core tube was lowered vertically over a plunger (rubber stopper) which extruded the sediment sample out the top of the tube. This technique minimized disturbance of the highly fluid sediment-water interface. All core samples were stored frozen, then thawed minimally and dried at 70°C, gently crushed in a mortar and pestle to loosen the dried aggregates, and sub-sampled for analysis of bioavailable phosphorus.

Phosphorus held in the particulate phase in sediments can be divided into the organic and inorganic phosphorus fractions. The latter fraction can be further separated into apatite phosphorus (AP) and non-apatite inorganic phosphorus (NAIP) components (Williams et al. 1976). The AP fraction is only slightly soluble and therefore essentially unavailable. The NAIP fraction is comprised mainly of inorganic phosphorus adsorbed on iron- and aluminum-hydrous oxides, and is highly correlated with "available P" (Williams et al. 1980). NAIP is estimated by a sequential extract-

ion procedure, using citrate-dithionite-bicarbonate (CDB reagent), NaOH, and HCl as reagents (Williams et al. 1976). In recent experiments using chemical fractionation and algal bioassay, the bioavailability of inorganic phosphorus in the different sediment fractions was determined. An extraction with 0.1 N NaOH using a soil/solution ration of 1:1000 (Williams et al. 1980) gave a complete extraction of bioavailable phosphorus, whereas some other methods gave an excess or incomplete extraction (Sonzogni et al. 1982). NaOH-extractable inorganic phosphorus (NaOH-IP) is thought to desorb from $\text{Fe}(\text{OH})_3$ -P complexes (Manning and Jones 1982).

Bioavailable phosphorus was determined following a NaOH extraction, as above, combining techniques outlined by Williams et al. (1980) and Mayer and Williams (1981) (see Appendix IV).

2.2.4 Total Phosphorus Content of Milfoil Tissue

Whole plants were uprooted, gently washed in lake water, measured for length of longest branch, separated into shoot and root portions, and immediately dried at 65°C. Dried samples were ground in a Wiley Mill (20 mesh), ashed for 5 h at about 500°C, extracted with HCl and analysed for total phosphorus content by a modification of the method of Olsen and Dean (1965).

3. RESULTS

3.1 Concentration Gradients of Inorganic Phosphate in Surficial Sediments

Concentrations of SRP were much higher in the sediment interstitial water than in the overlying bottom water. As shown in Figures 6a and 6b, SRP concentrations increased along a steep gradient from near-zero (not detectable) concentrations at the sediment-water interface to a maximum at about 12 cm (Fig. 6b) to 20 cm (Fig. 6a) depth in the sediment. Below the peak, concentrations decreased slightly down to 32 cm.

Concentrations of adsorbed bioavailable phosphorus (NaOH-IP) showed a maximum near the sediment-water interface (Fig. 6a) or slightly below the interface at 4 cm depth (Fig. 6b). Concentrations decreased along a steep gradient down to about 20 cm sediment depth (Fig. 6a) coinciding almost exactly with the position of the SRP gradient. The inverse trends in the concentration gradients of SRP and NaOH-IP were interpreted as suggesting that upward movements of SRP were induced by diffusion along a concentration gradient generated by precipitation in the oxidized surface layer of the sediments (Carignan and Flett 1981). The fact that the NaOH-IP peak occurred 4 cm below the interface in Figure 6b supports the diffusion-precip-

FIGURE 6

Vertical concentration gradients of dissolved (SRP) and adsorbed (NaOH-IP) phases of bioavailable phosphorus in a denuded sediment.

a) 14 May 1982

b) 12 August 1981

pitiation explanation as opposed to suggesting a significant increase in phosphorus sedimentation (Carignan and Flett 1981). Oxidation of metals such as iron can induce precipitation or adsorption of dissolved phosphate.

Over all sampling times and for both sediment conditions (weedbed and denuded), profiles of SRP were quite variable. This was reflected in the variability among replicate samples (Fig. 7). This type of variability is typical of interstitial water phosphorus (see, for example, Brock et al. 1982) and may reflect differences in composition of deposited materials as well as the effects of localized processes.

3.2 Summer/Fall/Spring Profiles of SRP

The shape of the concentration gradient of SRP in the upper 8 to 10 cm of the denuded sediment changed dramatically between late summer (August) and fall (October) or spring (June 1982) profiles (Fig. 8). Whereas summer profiles showed a steep increase in SRP with depth in the top 10 cm of the sediment (Fig. 8a), the fall and spring (1982 only) profiles showed little difference in concentration of SRP between interstitial water in the top 10 cm and the overlying bottom water (Fig. 8b, c).

In the weedbed sediment, a similar drop in SRP

FIGURE 7

Range of values of SRP encountered during a sampling event. Samples were collected 12 August 1981. For the weedbed (a), there were 14 replicates, and for the denuded sediment (b) there were 7 replicate profiles.

FIGURE 8

Temporal changes in the shape of SRP profiles
in the denuded sediment

a) mid-summer

b) fall

c) spring

Number of profiles (n)

Bottom water (Bw)

concentration in the top 8 cm of the sediment was observed between late summer and fall, but the difference was not as pronounced. Some SRP profiles collected about 8 to 12 cm from the milfoil root crown in September, October and the following May still showed the typical 'summer' profile in the top sediment layers (Figs. 9a, b, c). These SRP profiles showed concentration increases immediately below the sediment-water interface, and a SRP maximum at about 12-20 cm depth.

The loss of SRP in the upper sediment mixed layer in winter can be attributed to a decrease in heterotrophic activity (Goldhaber et al. 1977). This loss may not be observed in the surface sediments within milfoil root zones if factors unique to the rhizosphere are operative, such as the presence of special heterotrophic species or leaching from plant roots. Perhaps conversion of organic phosphorus to inorganic phosphate by heterotrophs is maintained through a longer season as a result of an interaction between the milfoil and bacteria. Diffusion rates may also be different within plant root zones.

FIGURE 9

Temporal changes in SRP profiles collected 8 to 12
cm from a milfoil root crown

- a) September 14
- b) October 16
- c) May 14

Each profile represents a single sample

Bw = Bottom water

3.3 Temporal Variability of Phosphorus in the Weedbed Sediment

Within the milfoil-colonized sediment, vertical concentration gradients of SRP were weak and concentrations were low. The mean SRP peak concentrations were less than $400 \text{ ug} \cdot \text{L}^{-1}$ for all but one week in July (Table 1). There was little variability in mean SRP profiles with time, with the exception of the mid-July sampling (Fig. 10a). The mid-July sampling is discussed later. The weedbed SRP data from Table 1 are plotted in Figure 10a.

Table 2 shows the results of a one-way analysis of variance used to indicate overall differences with time in mean SRP concentrations. In the top two sediment layers (0 to 8 cm and 8 to 16 cm) mean SRP concentrations exhibited significant nonhomogeneity of variance as determined by Levene's test (Dixon et al. 1981). In these cases, the Welch and Brown-Forsythe tests are reported. These statistics test the equality of several means without assuming the equality of variance in each group (Dixon et al. 1981).

There was a significant variation ($P < .01$) in mean SRP concentration with time in the top 16 cm of the weedbed sediment (Table 2). The source of this variation was the very high SRP concentrations measured in mid-July and the moderately high SRP concentrations measured

FIGURE 10

Temporal variability in mean SRP profiles

a) weedbed sediment

b) denuded sediment

Numbers indicate the sampling_date (1981)

1 - June 16	5 - August 12
2 - June 30	6 - September 3
3 - July 14	7 - September 22
4 - July 28	8 - October 9

Plotted points represent mean SRP concentration for the 8 cm depth intervals (see Methods section for explanation). Lines connect samples collected on the same date.

TABLE 1 Interstitial water SRP concentrations in the weedbed sediment: Mean concentration in $\mu\text{g}\cdot\text{L}^{-1}$, standard deviation (SD) and number of profiles (n)¹

Depth Interval (cm)	16Jn	30Jn	14Jy	28Jy	12Au	03Se	22Se	09Oc
0-8								
$\bar{x}$	86	89	419	92	156	138	141	56
SD	41	31	169	38	35	86	111	46
n	6	7	7	7	7	7	7	8
8-16								
$\bar{x}$	138	139	607	182	319	205	153	172
SD	95	50	283	128	132	87	105	104
n	6	7	7	7	7	7	7	8
16-24								
$\bar{x}$	143	179	287	187	295	173	106	162
SD	91	96	142	175	148	103	95	223
n	6	7	7	7	7	7	7	8
24-32								
$\bar{x}$	181	205	170	230	275	172	94	198
SD	162	152	99	196	125	145	65	285
n	6	7	7	7	7	7	6	8
32-34								
$\bar{x}$	243	240	130	178	273	123	19	324
SD	249	182	78	110	162	52	-	310
n	5	6	6	6	7	4	1	4

1 Each mean SRP value was derived as follows:

for samples collected 16 Jn to 03 Se, SRP values of duplicate samplers were averaged for each 2 cm depth

interval, then data were condensed, 4 compartments at a time, to give the depth intervals listed here. For example, $\bar{x}=139 \text{ ug} \cdot \text{L}^{-1}$ value for 30 Jn at 8-16 cm was derived from 56 (that is $7 \times 2 \times 4$) separate analyses. For samples collected 22 Se and 09 Oc, only 1 profile was collected per milfoil plant. Number of profiles (n) is less in the lower depth class (32-34 cm) since not all profiles were of equal length.

TABLE 2 Overall differences with time in mean SRP concentration in the weedbed, calculated for 5 sediment depth intervals

Depth Interval (cm)	Test	DF	Significance Level
0-8	Levene	7, 48	.01
	Welch	7, 20	.01
	Brown-Forsythe	7, 18	.01
8-16	Levene	7, 48	.05
	Welch	7, 20	.05
	Brown-Forsythe	7, 20	.01
16-24	ANOVA	7	not significant
24-32	ANOVA	7	not significant
32-34	ANOVA	6	not significant

DF - Degrees of freedom

TABLE 3 Pairwise comparisons of mean SRP concentration by Welch's separate variance t test, evaluated using Bonferroni probabilities^{1,2}

Depth Interval (cm)	Time	Overall Significance Level
0-8	14JY vs 16JN	.05
	14JY 090C	.05
	14JY 30JN	.10
	14JY 28JY	.10
	12AU vs 090C	.05
	12AU 30JN	.10
8-16	not significant	

1 For a Bonferroni probability, $p < \frac{\alpha}{n}$

For this data, there are $n=28$ pairwise comparisons. Therefore for the t test to have an overall significance level of .05, the P-value must be less than .00178. Likewise for $\alpha=.10$, $P < .00357$

2 Pairwise comparisons are performed when an overall difference was detected between means in Table 2

August 12. As shown in Table 3, the mid-July and August samplings in the top 8 cm of the sediment were most different from the spring (June) and fall (October) samples. This fits the summer/fall pattern of SRP profile differences in the top sediment layer discussed in Section 3.2.

While there was an overall difference in mean SRP values in the 8-16 cm interval indicated by the Welch test (Table 2), none of the pairwise differences were significant at the 10% level (Table 3). This can happen when the sample point falls outside the elliptical F region (the Welch test is a type of F test), but inside the polyhedral region formed from the all-pairs t tests (Miller 1966, p.91).

These results indicate that there was no significant variation in interstitial water SRP concentration in the weedbed sediment over the growing season, except in the top 8 cm layer. In this layer, there was a mid-July SRP maximum followed by a lesser peak in August.

Seasonal trends in the dissolved (SRP) and solid (NaOH-IP) phases of bioavailable phosphorus in the weedbed sediment are shown in Figure 11. The two phases are expected to vary similarly since they are assumed to be in a rapid equilibrium (Li et al. 1972). The lag between plotted points for SRP and NaOH-IP seen in Figure 11b is the result of the 1 week sampling difference. A close relationship was observed between SRP and NaOH-IP in the

FIGURE 11

Temporal changes in the dissolved (SRP) and adsorbed (NaOH-IP) phases of bioavailable phosphorus in the weedbed sediment

- a) 2 to 4 cm depth in sediment
- b) 12 to 14 cm depth in sediment
- c) 20 to 22 cm depth in sediment

NaOH-IP is in $\mu\text{g}\cdot\text{g}^{-1}$

SRP is in $\mu\text{g}\cdot\text{L}^{-1}$

P = phosphorus

12 to 14 cm depth interval, where both phases increased in mid-July (Fig. 11b), and in the 20 to 22 cm interval where both forms remained fairly constant with time (Fig. 11c). Near the sediment-water interface (2 to 4 cm depth), both SRP and NaOH-IP increased in mid-July, but SRP declined precipitously at the next sampling, whereas NaOH-IP continued to increase (Fig. 11a).

This lack of correspondence between the 2 phosphorus phases following the mid-July sampling (Fig. 11a) may have several possible explanations. Oxidizing conditions near the sediment surface result in preferential adsorption of phosphate on hydrated ferric oxides (Williams et al. 1976, 1980, Manning and Jones 1982). Adsorption of SRP released during mid-summer decomposition of organic matter could explain the steady increase in NaOH-IP throughout the summer. The very high SRP concentrations measured in mid-July are more difficult to explain. The data from this sampling are immediately suspect because they are higher than the corresponding mean SRP concentration measured at the same time in the denuded sediment. Mean SRP concentrations determined for the 0 to 8 cm and the 8 to 16 cm depth intervals were, respectively, 419 ± 169 and $607 \pm 283 \text{ ug} \cdot \text{L}^{-1}$ (weedbed, see Table 1) and 99 ± 72 and $377 \pm 135 \text{ ug} \cdot \text{L}^{-1}$ (denuded, see Table 4). In all other cases, weedbed SRP concentrations were lower than corresponding mean values in the denuded sediment. It is possible that some process interacting with milfoil

TABLE 4 Interstitial water SRP concentrations in the denuded sediment: Mean concentration in $\mu\text{g}\cdot\text{L}^{-1}$, standard deviation. (SD) and number of profiles (n)¹

Depth Interval (cm)	16Jn	30Jn	14Jy	28Jy	12Au	03Se	22Se	09Oc
0-8								
$\bar{x}$	115	35	99	86	119	274	190	3
SD	40	34	72	83	49	236	124	4
n	5	7	7	7	6	7	4	3
8-16								
$\bar{x}$	308	165	377	557	717	887	834	141
SD	150	144	135	233	266	320	230	47
n	5	7	7	7	6	7	4	3
16-24								
$\bar{x}$	464	266	460	888	809	903	940	475
SD	162	175	188	331	327	326	132	270
n	5	7	7	7	6	7	4	3
24-32								
$\bar{x}$	507	334	409	832	722	787	830	696
SD	134	155	256	368	362	292	180	411
n	5	6	7	7	6	7	4	3
32-38								
$\bar{x}$	496	418	311	693	643	712	713	496
SD	92	148	131	304	318	276	120	141
n	4	5	6	7	6	7	4	2

1 Each mean SRP value was obtained by condensing 4 SRP values determined for consecutive 2 cm depth intervals, for the number of profiles indicated (n).

roots in the upper sediment layers led to a pulse of SRP being released to the interstitial water in mid-July. The subsequent rapid decrease in SRP which occurred by the end of July (see Fig. 11a, b) would then have to be explained, perhaps as a result of adsorption on particulates, biological uptake, or release to the overlying water.

Alternatively, the mid-July sampling in the weedbed may be non-representative of the weedbed as whole, and represent a site-specific difference. While the mid-July SRP increase may represent a real trend, the magnitude of the variation may be non-representative. The exact location sampled in the weedbed on 14 July was not re-sampled, so the possibility of a site-specific difference can not be discarded.

3.4 Temporal Variability of Phosphorus in the Denuded Sediment

Within the denuded sediment, vertical concentration gradients of SRP were initially weak, but became quite pronounced by mid-summer, with peak mean SRP concentrations reaching 800 to 940 $\mu\text{g}\cdot\text{L}^{-1}$ (see Table 4). There was an obvious trend for mean SRP profiles to increase in concentration throughout the summer until October, when SRP concentrations decreased sharply, particularly in the upper sediment layers (Fig. 10b). Standard deviations for mean SRP values plotted in Figure 10b are

given in Table 4.

Table 5 shows the results of a one-way analysis of variance test used to indicate overall differences with time in mean SRP concentrations. At all depths in the denuded sediment, there was a significant variation in mean SRP concentration ($P < .05$), and the variation was highly significant ($P < .01$) between 8 cm and 24 cm depth. In the top 8 cm layer of the sediment, nonhomogeneity of variance of mean SRP groups was significant, and therefore the Welch and Brown-Forsythe tests were used to test for equality of the means.

The source of the overall variation between mean SRP groups is shown in Table 6. In the upper 16 cm of the sediment, the differences occurred between fall samples (09 October) and late summer samples (late July to early September), and between late summer samples and spring samples (June). In the 16 to 24 cm depth interval, differences occurred mainly between samples collected in June and in late September. In the 24 cm to 32 cm interval, no pairwise comparisons were significant at the 10% level although there was an overall significant difference ($P < .05$) in means (see Section 3.3 for explanation). In the 32 cm to 38 cm interval, the early summer (14 July) samples were significantly lower than samples collected at this depth in late summer (22 September).

These results indicate a strong pattern of very high

TABLE 5 Overall differences with time in mean SRP concentration in the denuded sediment, calculated for 5 sediment depth intervals

Depth Interval (cm)	Test	DF	Significance Level
0-8	Levene	7, 38	.01
	Welch	7, 15	.01
	Brown-Forsythe	7, 13	.05
8-16	ANOVA	7	.01
16-24	ANOVA	7	.01
24-32	ANOVA	7	.05
32-38	ANOVA	7	.05

DF - Degrees of freedom

TABLE 6 Pairwise comparisons of mean SRP concentration by Welch's separate variance t test, evaluated by Bonferroni probabilities^{1,2}

Depth Interval (cm)	Time	Overall Significance Level
0-8	090C vs 12AU 090C 16JN	.10 .10
8-16	16JN vs 03SE 30JN 12AU 30JN 03SE 090C vs 28JY 090C 12AU 090C 03SE	.10 .10 .05 .10 .10 .05
16-24	16JN vs 22SE 30JN 28JY 30JN 03SE 30JN 22SE 14JY 22SE	.10 .05 .05 .01 .05
24-32		not significant
32-38	14JY vs 22SE	.05

1 Bonferroni probabilities calculated as in Table 3

2 Pairwise comparisons are performed when an overall difference between means was detected in Table 4

SRP concentrations in interstitial water in mid- to late- summer, particularly between 8 and 23 cm depth in the sediment but also at higher and lower depths. SRP concentrations were lower in spring and in the fall (October).

Seasonal trends in the dissolved (SRP) and solid (NaOH-IP) phases of bioavailable phosphorus in the denuded sediment are shown in Figure 12. Both phosphate phases show similar trends with time. In the top layer of the sediment, SRP concentrations did not begin to increase until late August (Fig. 12a), whereas concentrations began increasing in early July at 12 to 14 cm depth (Fig. 12b), and in late July at 20 to 22 cm depth (Fig. 12c). SRP concentrations peaked in early September (Figs. 12a, b) or late September (Fig. 12c), then declined at all depths in October.

While SRP concentrations decreased between the 16 June and the 30 June sampling dates (Fig. 12, Table 4), this decrease may not represent a real trend. The 16 June samples were collected about 4 to 6 weeks after the sediment had been denuded of rooted plants. To test whether the 16 June 1981 samples registered effects of the disturbance created by denuding activities, the area was re-sampled on 18 June 1982, one year following plant removal. Mean SRP profiles for the two samplings are shown in Figure 8c. Significant differences between the 2 mean profiles occurred in the top (0 to 8 cm) layer and

FIGURE 12

Temporal changes in the dissolved (SRP) and adsorbed (NaOH-IP) phases of bioavailable phosphorus in the denuded sediment

- a) 2 to 4 cm depth in sediment
- b) 12 to 14 cm depth in sediment
- c) 20 to 22 cm depth in sediment

NaOH-IP is in $\mu\text{g}\cdot\text{g}^{-1}$

SRP is in $\mu\text{g}\cdot\text{L}^{-1}$

TABLE 7 Analysis of variance of mean SRP profiles
collected in the denuded sediment 16 June 1981 and
18 June 1982

Depth Interval (cm)	$F_{1,8}$	Significance Level
0-8	60.74	.01
8-16	0.26	not significant
16-24	2.58	not significant
24-32	17.31	.01

F - F statistic with 1 degree of freedom in the
numerator and 8 degrees of freedom in the denom-
inator

the lower (24 to 32 cm) sediment layer (Table 7), indicating that removal of the plants had caused mixing and homogenization of the surface sediments causing higher SRP values, and probably that recent colonization by plants had depleted the lower sediments of SRP in 1981. This result indicates that, in Table 6, the difference between October 9 and June 16 in the 0-8 cm depth interval represents a disturbance effect and not a temporal difference.

3.5 Spatial Variability of SRP Within Individual Milfoil Root Zones

Concentration gradients of SRP occurred laterally as well as vertically through the root volume of individual milfoil plants. Concentrations of SRP were lowest in interstitial water profiles collected nearest to the milfoil root crown, and profile concentrations increased with horizontal distance from the plant (Figures 13a, b, c, d). In Figure 13a, sample 5 which was furthest from the plant resembled the 'fall-type' profile described in Section 3.2. Of 9 lateral-vertical profiles of SRP measured in the root zone, 7 sets conformed to the pattern described above. Root effect was probably absent from the 'anomalous' profile shown in Figure 14, as the plant, when collected following interstitial water sampling, had only a few very short roots. Each sample clearly depends on the condition of the plant being sampled, and on the location of the sampler with respect to actively absorb-

FIGURE 13

Lateral-vertical SRP concentration gradients in a milfoil root zone. Each profile represents one sampler placed at a distance from the milfoil root crown as indicated in the inset.

- a), b) and c) samples collected 14 September 1981
- d) samples collected 06 October 1981

Bw = Bottom water

FIGURE 14

Anomalous lateral-vertical SRP profile collected
at the base of a milfoil plant. Samples were
collected 14 September 1981. Bw = Bottom water

ing roots.

The pattern of increasing SRP concentration with increasing distance from the plant was shown quite clearly when a set of samplers was run continuously between the root crowns of two adjacent milfoil plants (Fig. 15). The highest SRP concentrations occurred mid-way between the two plants. The lateral influence of these milfoil plants on interstitial water SRP extended over 4 samplers for the one plant and over 2 sampler widths for the other, i.e. a 20 cm and a 10 cm radius about the plants, respectively.

The vertical influence of milfoil roots can be inferred to extend down to the point at which the adjacent SRP profiles coincide. Extrapolation of the profiles in Figures 13 and 15 suggests that adjacent lines might have intersected anywhere from 38 cm depth (Figs. 13b, d) to 43 cm (Fig. 15) to 52 cm (Fig. 13a). Using longer samplers in May 1982, the intersection point of a set of adjacent profiles was measured at 56 cm depth in the sediment (Fig. 16), indicating that milfoil may be absorbing dissolved phosphate from deep within the zone of permanently buried materials. Whether this lateral-vertical profile is representative is not known, as it was the only root zone sampled in May. These SRP concentrations are almost twice as high as those measured in milfoil root zones the previous fall.

FIGURE 15

Lateral-vertical SRP concentration gradients collected along a continuous transect between adjacent milfoil plants. Samples collected 16 October 1981. Bw = Bottom water

FIGURE 16

Lateral-vertical SRP concentration gradients
collected at intervals between two milfoil
plants. Samples collected 14 May 1982.

Bw = Bottom water

3.6 Plant Responses: Temporal Variability in Tissue Phosphorus Content and Plant Height

Concentrations of total phosphorus contained in milfoil shoot tissue (percent dry weight) showed an early spring peak followed by a sharp decline, and then concentrations fluctuated somewhat throughout the summer (Fig. 17). This trend is typical for this species of milfoil (for example, Adams and McCracken 1974) as well as for other species of aquatic macrophytes (Wile and Hitchin 1977). By December 1981, concentrations of phosphorus in the unexpanded winter shoots were .13% ($n=5$), and by the next spring (15 May 1982), shoot phosphorus concentrations were again high at .24% ($n=2$).

In August, milfoil shoot phosphorus content approached low levels considered by Gerloff (1975) to result in growth limitation. Biomass was not measured, so it is not known if these low internal phosphorus concentrations actually resulted in reduced growth, but plant height (length of the longest branch) did not decrease (Fig. 17). Maximum milfoil biomass often occurs in August, for example in Lake Wingra (Carpenter 1980) and in Southern Chemung Lake (Wile and Hitchin 1973).

Plant growth, as indicated by increased length of the plant, was rapid in May and early June (Fig. 17). Milfoil grows rapidly to reach the water surface, and then branches at the surface forming a dense canopy (Grace and Wetzel 1978).

FIGURE 17

Temporal variation in milfoil tissue content of
phosphorus and in plant height

All plotted points are the mean value for 10 plants.
For plant % P, error bars represent 1 S.E.

4. DISCUSSION

4.1 Vertical Distribution of Bioavailable Phosphorus in Sediments

Pore water nutrient profiles are a sensitive indicator of the decomposition of organic matter. Organic matter is decomposed through bacterially-mediated oxidation-reduction reactions. With increasing depth in sediments, reduction reactions proceed in a sequence which is universally followed, with first O_2 , then MnO_2 and NO_3^- , Fe_2O_3 , and SO_4^{2-} being reduced during the oxidation of organic carbon (Froelich et al. 1979). This order reflects decreasing energy production per mole of organic carbon oxidized. Dissolved phosphate is released during the decomposition process, so interstitial water SRP concentrations will increase when decomposition occurs, with a local SRP maximum forming where decomposition rates are highest. The rate of decomposition varies with temperature and depth (Goldhaber et al. 1977), the depth factor reflecting the decrease of bacterial populations and metabolizable organic matter with increasing depth in the sediment (Lerman 1979).

SRP released during decomposition may undergo reversible linear adsorption (Bernier 1977), or be redistributed through diffusion (Carignan and Flett 1981). In the denuded section of sediment in Lake Opinicon, the SRP concentration maximum occurred between about 12 and 20 cm

depth, and closer to 12 cm depth in the weedbed sediment. Diffusion of SRP in pore waters occurs along concentration gradients away from the SRP concentration maximum, both upwards to the overlying water and downwards in the sediment. The increase in adsorbed bioavailable phosphorus which occurred near the sediment-water interface (see Fig. 6) indicates that SRP in the reduced sediments had diffused upward and been adsorbed in the oxidized surface layer of the sediments (Carignan and Flett 1981). This removal of SRP from solution would considerably slow the rate of SRP diffusion near the interface. The net result is that bioavailable phosphorus, both dissolved and adsorbed, is not evenly distributed with depth in the sediment. Adsorbed bioavailable phosphorus is most plentiful within the top 5 cm of the sediment, while dissolved bioavailable phosphorus is highest between 12 and 20 cm depth in the sediment. It is possible that this pattern might lead to some spatial partitioning of zones exploited for phosphorus uptake by different forms of rooted aquatic plants, and will be discussed later.

4.2 Temporal Distribution of Bioavailable Phosphorus in Sediments

In Lake Opinicon, the supply of bioavailable phosphorus (SRP + NaOH-IP) above 38 cm in the denuded sediment increased significantly during the summer, peaking in August and early September. During the late summer, organic matter decomposition rates are typically maximal, partly because of high temperatures and high sedimentation rates of organic matter, and also maximum development of bacterial populations might be expected. This would result in maximal production of SRP.

With the onset of cool temperatures in October, the steep SRP gradient in the upper 10 cm of sediment disappeared, so that interstitial waters in this layer were indistinguishable from the overlying water with respect to SRP concentrations. This condition persisted in SRP profiles measured the following spring (June). Similar differences between summer and winter SRP concentrations in the upper 8 to 10 cm of sediments in Long Island Sound were attributed to a lowering of bacterial metabolic rates thus reducing decomposition (Goldhaber et al. 1977). As decomposition diminishes, sediments would become less reducing, that is, more oxidizing, and SRP might be preferentially removed from solution through adsorption/precipitation reactions. Inorganic uptake of phosphorus coupled with lowered production of SRP could produce the low SRP values.

A study of temporal variations in the upper 6 cm of an estuarine sediment (Hines et al. 1982) showed that dissolved phosphate concentrations in the pore water increased in mid-May coincident with increased heterotrophic (bacterial) activity, and then decreased in late May to early June when bioturbation activity increased. Bioturbation effects include the flushing of nutrient-rich interstitial water up into the overlying water as a result of irrigation activities of burrowing organisms (Goldhaber et al. 1977), and the mixing of nutrient-poor lake water into the upper interstitial water. My results showed that, from June to mid-August, there was no increase in dissolved phosphate (SRP) in the 2-4 cm layer of the denuded sediment, while deeper in the same sediment between 12-14 cm SRP concentrations began increasing at the end of June. It is possible that bioturbation effects influenced the surficial sediment SRP concentrations during June and July. In July 1980, Keast (1983) found significant numbers of large bloodworms (Chironomus spp.) in the benthos of the M. spicatum sediment. However, 'burrowing' is probably an inappropriate description of benthic activity in these very fluid, fine-grained sediments.

While the supply of bioavailable phosphorus increased significantly in the denuded sediment during the summer, no significant variation was measured in the weedbed sediment below 8 cm. This demonstrated that milfoil root

uptake fully utilized the increased phosphorus supply, as both the dissolved (SRP) and adsorbed (NaOH-IP) fractions remained depleted (Fig. 11b, c) compared to the denuded sediment (Fig. 12b, c). Root uptake of phosphorus is not expected to be significant in the upper 4 cm of the sediment for milfoil (Prentki 1979), nor does the temporal pattern of SRP concentration in the denuded and weedbed upper layers (2-4 cm) suggest that plant utilization of SRP and NaOH-IP occurred.

The greater availability of bioavailable phosphorus, and particularly SRP, in these sediments in summer than in the spring, suggests that root uptake should be more important to milfoil later in the summer. Denny (1972) suggested that submerged plants should derive their nutrients from the source of greatest availability. Usually this is the sediments, except where lake waters are hypertrophic. Late in the ice-covered period of early spring, average phosphorus concentrations in lake water may be high, as observed in Shagawa Lake, Minnesota (Larsen et al. 1981).⁴ This phosphorus would be available for foliar absorption by submerged macrophytes such as milfoil, which maintains an evergreen root crown over winter, and grows rapidly to the water surface following ice-out. Snowmelt may also supply phosphorus to littoral waters, although Prentki et al. (1979) noted surface layering and movement of snowmelt

waters which prevented any interception by the plants which were below the surface at that time of year.

Generally, lake waters of Lake Opinicon have low concentrations of total phosphorus, averaging about $20 \mu\text{g}\cdot\text{L}^{-1}$ (Ontario Ministry of Environment 1971), and SRP concentrations in the littoral bottom water were low or not detectable in my study. In comparison, SRP in the interstitial waters of the sediments was over 20 times higher. This large difference in phosphorus availability between the sediments and the open water allows one to predict (Carignan 1982) that root uptake of phosphorus by milfoil should be more important than shoot absorption in Lake Opinicon, perhaps in the order of 80% root uptake. In mesotrophic Lake Memphremagog, milfoil obtained all its phosphorus from the sediments (Carignan and Kalff 1980).

4.3 Spatial Influence of Milfoil Roots in the Sediment

The existence of both lateral and vertical SRP concentration gradients in the interstitial water in a milfoil root mass clearly demonstrated that the plants were absorbing SRP through their roots, and thus depleting interstitial water SRP. Depletion effects were measured down to 56 cm depth in the sediment. The average root length for milfoil in mid-summer was 46 ± 10 cm ($n=55$). Allowing that the finer roots would be

broken off when the plant was uprooted, milfoil could be expected to absorb nutrients down to 50 cm. In Lake Wingra sediments, peak root development of milfoil occurred between 6-15 cm depth, with rapidly decreasing numbers of roots down to 35 cm (Prentki 1979). Much longer milfoil root development was observed by Young (1973) in a Tennessee reservoir, where the thick rhizome masses penetrated the entire depth of the substrate layer (20-60 cm) and extended through the underlying regolith. The length and development of a milfoil root system will depend on substrate conditions, as well as other factors.

The depths from which rooted aquatic plants draw their nutrients has important implications for nutrient cycling in the littoral zone. Since nutrients below the sediment surface mixed layer are lost to the phytoplankton production cycle, the upward transfer of nutrients and their release to the overlying waters could stimulate algal production. I have demonstrated that milfoil absorbs phosphorus from deep within the sediment (down to 30-50 cm). Other studies have shown that sediment-derived phosphorus is translocated in milfoil to the shoot (for example, Barko and Smart 1980). When the plants undergo annual dieback, the phosphorus held in above-sediment biomass is released as SRP pulses to the surrounding water (Landers 1982) where it can stimulate algal growth. The plants can thus act as a mechanism

for internal phosphorus cycling, and the effect can be substantial within a lake having dense macrophyte populations (Prentki et al. 1979, Welch et al. 1979, Jacoby et al. 1982).

The lateral extent of SRP depletion contours around a milfoil root crown was about 10-20 cm. For the larger radius, plants would need to be spaced at least 40 cm apart to avoid interference between the roots of adjacent plants over SRP supplies. In the weedbed, milfoil clumps were generally spaced about 50 cm apart, which suggests that avoidance of intraspecific competition in the root zone may be a factor affecting the spacing of plants.

Harper (1977) noted that, while there is no indication that roots of different plants interfere, the innate differences in root form of different species growing together may suggest this. Milfoil and Vallisneria have very different growth forms and very different root forms. While milfoil may partially replace Vallisneria as a community dominant in some lakes, the two species may coexist (Titus and Adams 1979), as was observed at the study site. Milfoil has a long fibrous root mass, while Vallisneria has a shallow root system of rosette form, which Spence (1982) suggested is correlated with low-nutrient environments. The uneven vertical distribution of bioavailable phosphorus observed in sediments in this study suggests that a spatial partitioning of zones exploited for phosphorus absorption.

might occur. Milfoil roots extend down through the levels of high SRP availability, while Vallisneria roots are limited to the top 15 cm of sediment (as suggested by average root length of several specimens) where SRP concentrations are lower. This pattern suggests partitioning may occur. However, Vallisneria roots often intertwine with milfoil roots near the surface, so it may be that roots are randomly spaced with respect to separate plants, which supports Harper's (1977) contention that roots of different plants don't interfere. Taken further, this might suggest that factors in the root environment are not limiting.

In soils, the mobility of phosphate ions is extremely low and steep depletion contours appear near absorbing root surfaces (Harper 1977). In sediments, phosphate mobility may be higher due to the high water content and reducing conditions, but depletion contours were still measured. Local depletion of phosphate in the interstitial water caused by root absorption would be replenished by release of adsorbed phosphorus or by diffusion.

4.4 A Contradiction

Measurements of bioavailable phosphorus concentration in the denuded sediment indicated that the environmental availability of phosphorus was greatest in late summer. Similar measurements in the weedbed sediment indicated that this seasonal supply was being fully utilized by the milfoil. Yet at the same time, concentrations of total phosphorus in plant shoot tissue approached low levels considered by Gerloff (1975) to result in growth limitation. Internal phosphorus concentrations above Gerloff's (1975) 'critical level' are considered to be luxury consumption, since they are additional to the phosphorus immediately required for plant growth. Milfoil biomass is high in August, so low internal phosphorus concentrations may result from redistribution of phosphorus during growth. It is also possible that luxury phosphorus may be shed when environmental availability of phosphorus is high, or that internal phosphorus concentrations are not very meaningful. In Lake Wingra, milfoil approached internal phosphorus limitation and many plants died, but a factor other than depletion of external sediment and/or water reserves was thought to be involved (Smith 1979).

If the low internal phosphorus concentrations in milfoil truly indicate that the plants were growth limited during the latter part of the summer, then

levels of bioavailable phosphorus may have been insufficient to meet the plants' requirements. There is little quantitative information on what levels of bioavailable phosphorus are limiting. Williams et al. (1980) suggested that below about $250 \mu\text{g}\cdot\text{g}^{-1}$ P (as NAIP) there was little algal cell growth in a culture. Below about 16 cm in the milfoil sediments, bioavailable phosphorus levels were usually less than $200 \mu\text{g}\cdot\text{g}^{-1}$, but were considerably higher towards the sediment-water interface.

During August, the older milfoil branches were heavily coated with epiphytes and were beginning to fragment, and new green shoots were growing up from the root crown. Since milfoil does not provide a significant amount of phosphorus to its epiphyton (Carignan and Kalff 1982), the phosphorus being absorbed by milfoil roots must have gone into production of new shoots.

The milfoil weedbed failed to flower in 1981, and has been declining in density over the last few years. Lack of inflorescence formation was attributed to nutrient limitation in an emergent macrophyte, Cyperus esculentus (Barko and Smart 1979). However, Crowder et al. (1977) noted that patchy flowering in perennials such as milfoil and some potamogetons might be the result of even-aged clumps of plants.

5. CONCLUSIONS

1. Bioavailable phosphorus phases (dissolved and adsorbed) were unevenly distributed with depth in the sediment.
2. SRP profiles were consistent with organic regeneration and with the effects of inorganic uptake as a result of oxidation effects near the sediment-water interface.
3. NaOH-IP profiles were consistent with upward migration and inorganic uptake of dissolved phosphate near the sediment-water interface.
4. Bioavailable phosphorus (SRP) concentrations were maximal in late summer in the denuded sediment.
5. Root uptake of phosphorus by milfoil was demonstrated by lower bioavailable phosphorus concentrations in the weedbed sediment compared to the denuded sediment, and by the existence of depletion contours of SRP in milfoil roots.
6. SRP depletion contours associated with milfoil roots extended to depths of 50 cm in the sediment, and laterally to 20 cm about the plant.
7. Milfoil shoot tissue phosphorus concentrations showed a seasonal pattern that is typical for this species but the concentrations were quite low.

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APPENDIX I Equilibration characteristics of the dialysis sampler (Hesslein 1976), and the effect of differing pre-treatment schedules

Experiment I

A total of 32 vertical profiles of interstitial water were collected and analysed for soluble reactive phosphate (SRP). These samples represented 4 different equilibration times in situ and 2 pre-treatment conditions. Prior to insertion in anoxic lake sediments, the samplers were either deoxygenated in a closed water bath through which nitrogen gas had been bubbled, or were left oxygenated. Replicate samplers² were equilibrated in situ for 6, 14, 20 or 27 days, and all samplers were collected on the same day.

Multivariate analysis of variance (Dixon et al. 1981) indicated that there was no difference in SRP concentration attributable to either length of equilibration time nor to the type of pre-treatment condition.

Experiment II

A total of 12 vertical profiles of interstitial water were collected representing oxygenated and deoxygenated pre-treatment conditions, and equilibration times of 2, 5 and 10 days in situ. Samples were analysed for SRP, and data for depth intervals 4-6 cm, 8-10 cm, 12-14 cm, 16-18 cm, 20-22 cm, 24-26 cm, and 28-30 cm were

analysed statistically by a two-way analysis of variance. There was no difference ($P > .05$) in SRP concentrations in the sampler compartments attributable to length of equilibration time in the sediment. However, concentrations of SRP were higher for the oxygenated samplers between 8 and 16 cm depth in the sediment ($P < .05$). At the depths above 8 cm and below 16 cm, there were no differences in SRP concentration attributable to pre-treatment conditions.

Discussion

The lack of an effect on SRP concentration attributable to equilibration times ranging anywhere from 2 to 27 days indicates that equilibration was occurring in times equal to or less than 2 days. This result is not surprising as the high porosity (water content) of the sediments being sampled would enhance diffusion rates of molecules such as phosphate.

It is perhaps more surprising that the oxygenated samplers were not different from the deoxygenated ones (Experiment I), or only differed between 8 and 16 cm depth (Experiment II). The introduction of oxygen into anoxic sediments could have several possible effects. Oxidation of iron dissolved in the interstitial water leads to precipitation of ferric ions, with coprecipitation or adsorption of phosphate ions, so a decrease in SRP would be expected. Alternatively, oxygen could

temporarily accelerate decomposition processes leading to a release of phosphate. This might be expected to be especially noticeable in late summer when decomposition of organic matter is occurring at a high rate and availability of oxidants may be limiting. This latter effect would explain the increased SRP concentrations observed in the 8 to 16 cm depth interval. These samples were collected in early September. The sample size was small so no firm conclusions can be drawn. For longer equilibration times oxygenation effects were not observed.

Where dissolved iron concentrations are less than $100 \text{ ug}\cdot\text{L}^{-1}$, the iron apparently is not affected by atmospheric exposure (Lyons et al. 1979). Dissolved iron concentrations in the interstitial water samples collected for Experiment II varied considerably between samples, but were mainly between $100\text{-}200 \text{ ug}\cdot\text{L}^{-1}$, so dissolved iron may not be affected by oxygenated samplers. Similarly SRP would not be affected if the dissolved iron was not affected.

Schindler et al. (1977) found that binding of phosphate was not significantly affected by the presence or absence of oxygen in a lake in which no iron-phosphate minerals were detected. The mineral status of sediments in the present study was not determined.

APPENDIX II Effects of acidification and storage time on concentrations of dissolved phosphate (SRP)

The small 10 ml sample volume of interstitial water samples precluded repeated analysis (manual method) of the same sample to determine the effects of sample treatment and storage time. Instead, a number of samples were run under varying conditions and the results of these determinations were summarized.

Acid (H_2SO_4) may be added to preserve water samples (Henriksen 1969) and/or to prevent oxidation and precipitation of metal compounds, and to reduce adsorption on the surface of the container (German Chemists Association 1981). However, acidification may lead to hydrolysis of dissolved organic phosphorus compounds in the sample (Henriksen 1969, Stainton et al. 1977), so that SRP is overestimated. Long-term storage of samples often results in loss of dissolved components from the sample, and in an increase in the variability (scatter) in determinations (MacDonald and McLaughlin 1982).

SRP was determined for samples before and after the addition of acid, and following short-term and long-term storage of samples. Results were analysed by the paired-sample t test (Zar 1974).

Interpretation of the statistical results is ambiguous. The effect of adding acid was to cause a slight decrease in the concentration of SRP in the sample. A

small SRP decrease was also measured following storage up to 24 days. However, samples analysed after 6 days storage and again after 7 months storage showed an increase in SRP concentration, as did samples analysed after 8 months storage and 11 months storage. The opposite trend was expected.

Quantitatively, the change in SRP concentration in a given sample was not large. The difference between acidified and non-acidified sub-samples analysed the same day is less than 3%, and may in part reflect a dilution effect from adding extra liquid (acid) to the sample. Differences between samples re-analysed on different days can be attributed partly to the effects of recalibration with different blanks.

Differences greater than 10% are generally considered to represent real changes in a sample (German Chemists Association 1981), which assumes that the recurrent standard deviation of the test methods applied is less than $\pm 10\%$. Using this criterion, the differences observed between acidified and non-acidified samples and between samples analysed within 24 days are not real differences. Storage times of 7 months did result in real differences (mean=13%, range 1%-34%) in measured SRP in some samples, and generally increased the variability in the determinations.

APPENDIX III Construction details for building
the cylindrical dialysis sampler

Individual vials ('stackers') have ports on 3 sides. Dialysis membrane was wrapped around the stacker, glued along one side (Goodyear Pliobond Glue), and secured at the ends using O-rings. The stacker was filled and emptied by syringe through the rubber septa in the ends. In Figure A, the wide bands represent the positioning of holes in the plexiglas sleeve. The main section of sleeve held 10 stackers, and the extension unit held 7 stackers.

APPENDIX IV Procedure for NaOH-extractable phosphorus (Bioavailable)

Extraction

25 mg of dried sediment was shaken overnight in 50 ml of 0.1 N NaOH / 1.0 M NaCl in glass bottles, then transferred into centrifuge tubes and spun at about 2000 rpm for 15 minutes

Colour Reaction

Ingredients for the standards and samples were as follows:

<u>Standards</u>	<u>Sample</u>
5.0 ml standard	12.5 ml sample
12.5 ml 0.1 N NaOH/1 M NaCl	0.5 ml 6 N HCl
0.5 ml 6 N HCl	2.5 ml 4 N H ₂ SO ₄
2.5 ml 4 N H ₂ SO ₄	2.5 ml 0.96% molybdate
2.5 ml 0.96% molybdate	5.0 ml H ₂ O
2.0 ml ascorbic acid/tartrate	2.0 ml ascorbic acid/ tartrate
<u>25.0 ml</u>	<u>25.0 ml</u>

Samples and standards were read at 890 nm

Standards used were Blank, 0.1, 0.2, ..., 1.0, 1.2, 1.4, 1.6, and 1.8 ppm P

Phosphorus stock solution was 100 ppm P in 0.2 M HCl

Colour reagent was made of equal volumes of 10% ascorbic acid solution / .667 g with 250 ml tartrate solution.

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